


## RESEARCH ARTICLE

# Variable shifts in bird and bat assemblages as a result of reduced-impact logging revealed after 10 years

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**Handling Editor:** Raquel Carvalho**Abstract**

1. Selective logging is the most widespread driver of land-use change in biodiverse and carbon-rich tropical forests. However, the effects of selective logging on biodiversity are less than those associated with other drivers of forest degradation. A suite of recent research has shown that reduced-impact logging (RIL) results in few or no changes to biological assemblages. But because this logging technique is relatively new, most studies have only considered short-term impacts.
2. We address this research gap by quantifying changes in biodiversity assemblage as a result of RIL over the longer term. We comprehensively sampled bird and bat assemblages pre-logged, 1 year after, and 10 years after RIL in Guyana, using a before-after control-impact (BACI) sampling design. We compared bird and bat assemblages in each timeframe, and additionally appraised the impact of time since logging, and the number of trees harvested across the suite of species which we further divided between different feeding guilds, disturbance sensitivity and vertical stratification of forest use.
3. We found that 1 year after logging only minor changes could be detected, but 10 years later richness had slightly declined in some groups, while others had shown complete recovery. Nectivorous and insectivorous birds, and carnivorous bats declined in richness, while carnivorous birds, showed a clear recovery to a state akin to pre-logging. This indicates that for some niches a subtle, but long-term relaxation effect may be occurring, whereby extinction debts are realized long after the initial disturbance, while other groups have either recovered or not changed after logging.
4. Assemblage changes were also predicted by vertical stratification of forest use, with avian species using the understorey and mid-upper levels of the forest being most affected.
5. *Synthesis and applications:* Our study demonstrates how best practice forestry and logging can maintain healthy vertebrate populations over the long term. Forestry

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concessions that adopt techniques of low-harvest RIL and are managed for their long-term timber provision through extension of regeneration times beyond 10 years after harvest, are likely to benefit from the ecosystem services provided by biodiversity, while also making a valuable contribution to the global conservation estate.

#### KEYWORDS

extinction debt, forestry, Guyana, logging, reduced-impact logging, tropical rainforest

## 1 | INTRODUCTION

An estimated 400 million ha (~25%) of tropical rainforests are managed with the primary objective of producing timber via selective logging (Groenendijk et al., 2017). Selective logging, as opposed to clear-cutting, involves the removal of only high value timber species but many remain poorly managed with a lack of emphasis on minimizing the long-term negative impacts on the residual forest stand (Ansell et al., 2011; Edwards et al., 2012). The cost-effectiveness of long-term timber harvesting of selectively logged rainforests poses an obstacle to how well ecosystem integrity will be maintained (Boltz et al., 2003). Long-term harvesting requires several decades between cutting cycles that allow for intervals of regeneration, but depends on the strict management of logging concessions between these cutting cycles to prevent conversion and/or re-allocation (Bicknell, Gaveau, et al., 2015; Bicknell, Struebig, & Davies, 2015). As such, management that ensures the safeguarding of timber for future cycles remains an important requirement for retention of rainforests and their biodiversity.

Another key determinant of the long-term sustainability of selectively logged forests is the forestry technique. Conventional logging often leads to reduced forest heterogeneity, lower canopies, large forest gaps, an increase in carbon emissions and reductions in biodiversity (Bicknell, Phelps, et al., 2014; Bicknell, Struebig, et al., 2014; Foody & Cutler, 2003; Putz et al., 2012). An alternative to conventional forestry is the adoption of reduced-impact logging (RIL). RIL focuses on several activities such as pre-harvest inventories, planned road networks and the implementation of directional felling (Bicknell, Gaveau, et al., 2015; Bicknell, Struebig, & Davies, 2015; Macpherson et al., 2010; Putz et al., 2012). When compared to conventional selective logging, RIL consistently has lower impacts on forests (Hammond et al., 2000) and reduce carbon emissions associated with logging (Griscom et al., 2019; Putz et al., 2008; Umanay et al., 2019). Indeed, three decades of research has demonstrated that RIL helps minimize changes in wildlife assemblages compared with conventional techniques (e.g. Bicknell, Gaveau, et al., 2015; Bicknell, Struebig, & Davies, 2015; Putz et al., 2008). Some studies have demonstrated that RIL often has little or no effect on the assemblages of large mammals (Mayor et al., 2015; Roopsind et al., 2017) birds and bats (Azevedo-Ramos et al., 2006; Bicknell, Phelps, et al., 2014; Bicknell, Struebig, et al., 2014; Castro-Arellano et al., 2009), invertebrates (Bicknell, Phelps, et al., 2014; Bicknell, Struebig, et al., 2014; Davis, 2000) and amphibians (Donnelly et al., 2005; Ofori-Boateng et al., 2013). However, because RIL is a relatively modern technique, these studies have been conducted more

or less immediately after logging, leaving a gap in our understanding of species responses to RIL over the long term. This is important to explore not only for species conservation, but also because wildlife, and particularly mobile vertebrates such as birds and bats, provide services that benefit timber production such as seed dispersal and predation of pests (Corlett, 1998; Kremen et al., 2007; Schleuning et al., 2011; Sekercioglu, 2006). Both birds and bats are therefore vital to the longevity of a logged rainforest.

Behavioural responses of vertebrates to disturbance contribute to how well we can gauge disturbance recovery (Dodd et al., 2012; Gray et al., 2007). Indeed studies of both birds and bats indicate that richness in logged rainforests is dependent on feeding guild (Bonaccorso & Gush, 1987; Gray et al., 2007), vertical stratification of forest use (i.e. canopy, mid-levels, understorey etc (Asner et al., 2004; Kalko & Handley, 2001); as well as the intensity of timber harvesting (Asner et al., 2004; Burivalova et al., 2014). Some studies addressing bird responses to selective logging found that insectivorous birds experienced a greater decline after logging compared to other bird feeding guilds (Gray et al., 2007; Owionji & Plumtre, 1998; Powell et al., 2015), whereas others have reported the opposite (Cleary et al., 2007; Edwards et al., 2012). Similar studies have found that canopy species may be most sensitive after RIL due to breaks in the canopy from logging (Felton et al., 2008), with frugivorous species being the most affected (Chaves et al., 2017). Others have found that mid-lower stratification sensitivity increases with changes in rainforest microclimate with regeneration (Blonder et al., 2018). Species may also adapt their foraging behaviour, for example mixed-flock foraging, to allow some bird species to fill broader feeding guilds in logged rainforests (Srinivasan, 2019), making them more resilient to changes in the resource base that may result from logging. Bats in the subfamily Phyllostominae have been shown to be sensitive to rainforest disturbance (Medellín et al., 2000; Willig et al., 2007) and tend to have greater access to fruit, pollen, nectar and invertebrates in early-mid-stage successional rainforest habitats (Castro-Luna et al., 2007). Furthermore, bat assemblage studies have shown spikes in frugivore abundance in logged rainforest habitats, due to pioneer fruiting tree dominance (Castro-Arellano et al., 2009; Ethier & Fahrig, 2011), whereas carnivorous bats have been described as being sensitive to late-stage logged rainforests, possibly due to prey species change (Clarke et al., 2005). We predict both birds and bats would respond accordingly to changes in their environments, sometimes via shifting their dietary composition and stratification of forest use due to resource availability changes that

occur in regenerating forests following harvest. Thus, quantifiable changes in richness as regeneration time increases, may be observed as a result of shifts in dietary composition and stratification of forest use.

Continual sampling of bird and bat assemblages allows for long-term temporal analysis of changes in species composition and abundance, and thereby revealing subtle changes that may otherwise go undetected. To date, most studies regarding the impacts of RIL on biodiversity have been over relatively short-term periods (~1–3-year post-logging). Here, we explore the longer-term effects of RIL on bird and bat assemblages over multiple sampling occasions. As such, we employ a before-after control-impact (BACI) design, to offer temporal comparisons between three timeframes (pre-logged, 1 year after and 10 years after logging).

## 2 | MATERIALS AND METHODS

This field study was authorized through the Environmental Protection Agency (EPA) under permit number 112619 BR 016 and in accordance with Guidelines for Biodiversity research in Guyana and the Environmental Protection Act 1996. Ethical approval was not required for this field study.

### 2.1 | Study site and logging approach

We sampled bird and bat assemblages in the Iwokrama Forest in central Guyana, South America. The Iwokrama Forest is a 3710 km<sup>2</sup> (371,000 ha) lowland terra firme rainforest that is divided into two main areas: a sustainable utilization area and a wilderness preserve. The sustainable utilization area is used to test and practice improvements to forestry in tropical forests. The adjoining wilderness preserve acts as a no-disturbance buffer zone area, intended for strict conservation and research. Selective logging in Iwokrama uses RIL methods. This involves a polycyclic silvicultural harvesting approach targeting approximately 20 tree species. Timber operations are certified under the Forest Stewardship Council (FSC). To avoid large canopy openings and ensure minimal forest damage, a pre-harvest inventory is conducted before timber extraction. This is then followed by planned skid trails of predetermined length and width, directional felling of target trees (minimum 40 cm diameter) and removal of linked vines to avoid connected trees being pulled down along with target trees. Mean logging intensity in the Iwokrama rainforest is 3.2 trees ha<sup>-1</sup>, representing approximately 6.3% of trees above 40 cm diameter (Bicknell, Gaveau, et al., 2015; Bicknell, Struebig, & Davies, 2015).

### 2.2 | Experimental design

We used a BACI study design, incorporating the procedure in Bicknell, Gaveau, et al. (2015) and Bicknell, Struebig, and Davies (2015) from

the same site as the best way to detect assemblage changes from disturbance (Christie et al., 2020). Three 'timeframes' were included in this study design: pre-logged, 1 year after and 10 years after RIL. Data on pre-logged and 1 year after were collected between 2008 and 2013 and are presented in Bicknell, Gaveau, et al. (2015) and Bicknell, Struebig, and Davies (2015). We resurveyed these sites 10 years after, between 2020 and 2021. Our final dataset represents 14 logged sites each surveyed in each timeframe: pre-logged, 1 year after and 10 years after logging. Over the same time periods we also surveyed three control sites, situated in a remote, undisturbed area 16 km from the logged sites and never underwent logging. All sites were a minimum of 1 km from one another. Sites were positioned at least 500 m from unlogged areas post-logging, however, this varied in the different timeframes, in those 10 years after logging more of the surrounding area had been logged than at 1 year after logging. Before logging, all sites had no evident human disturbance.

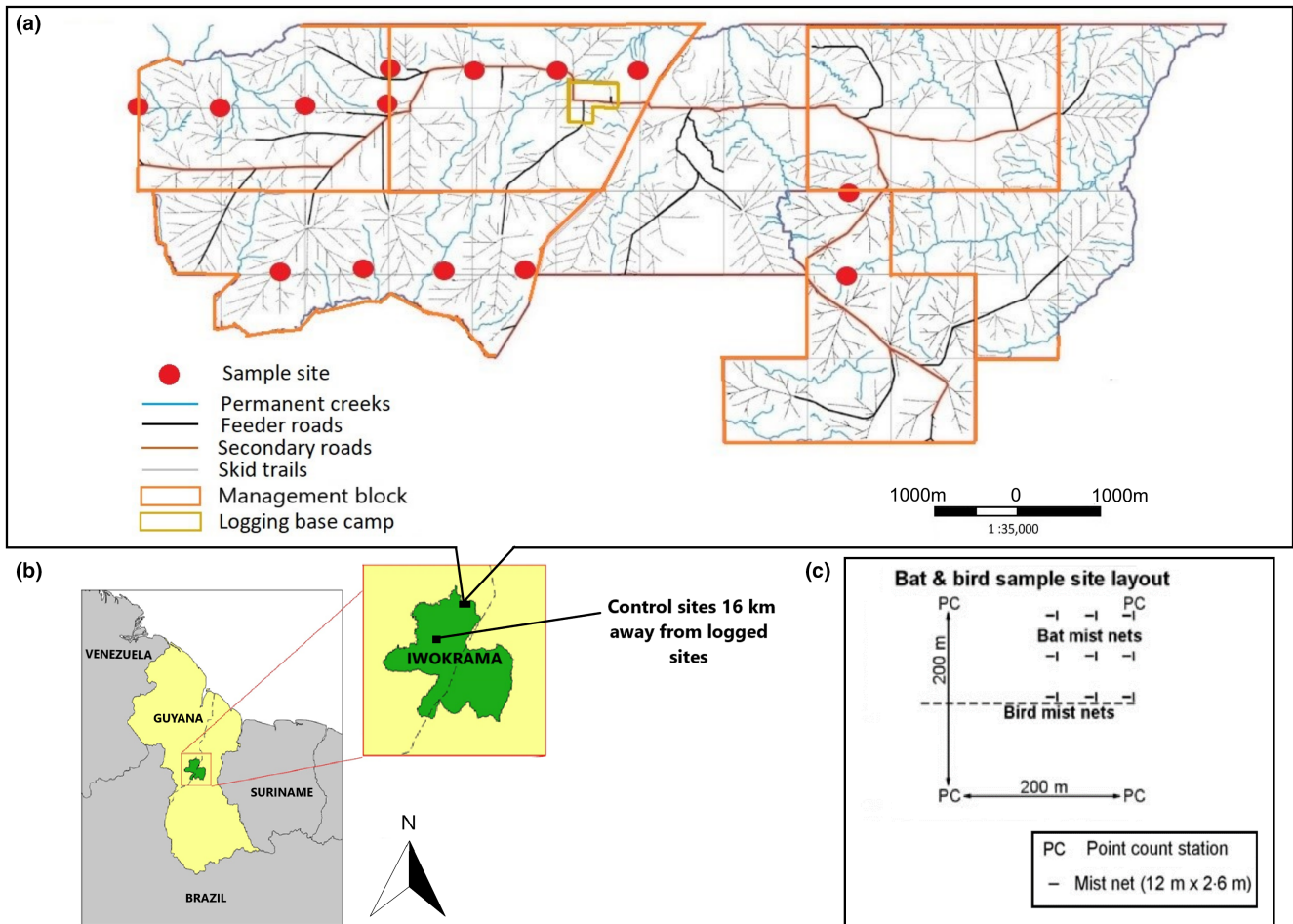
### 2.3 | Bird and bat sampling

To sample at different vertical stratifications of forest use, we adopted two methods to sample the bird assemblage. We used ground-level mist nets to sample the understorey bird assemblages (occasionally some species that occupy higher forest levels were also recorded), and point counts were used to sample birds at all stratification levels. Eighteen mist nets (12 × 2.6 m, mesh size 36 mm), were set along a straight line. Four-point count stations were established at the corners of a 200 m grid and were done by the same, experienced observer to minimize observer bias. We also sampled bat assemblages using understorey mist nets (12 × 2.6 m, mesh size 36 mm). Eighteen mist nets for bats were positioned throughout a 100 m × 100 m grid in pairs, spaced every 50 m (Figure 1).

Mist netting was done from 06:00 am to 18:00 for birds, and from 18:00 to 00:00 for bats. Bird point counts were carried out between 05:30 and 07:30. These were conducted for three consecutive days for a total of 2 months at the beginning and end of the year (approximately 21 sample days per month) to maintain consistency of all sample years being outside of Guyana's wet season, but an additional day of sampling was sometimes added in the event of bad weather to ensure approximately consistent sampling effort at all sites. Additionally, we avoided (to the best of our ability) netting during full moon nights as bat activity has been known to drop during full moon cycles (Santos-Moreno et al., 2010).

### 2.4 | Species identification and guild specification

The field team was trained and experienced in species identification and handling of birds and bats. All point counts were done by an experienced observer and audio IDs were cross-checked using Merlin® (Cornell Lab of Ornithology 2023). Species identification of birds was done using regional field guides (Ascanio et al., 2017; Restall et al., 2006). Where there was any uncertainty, pictures and



**FIGURE 1** (a) Location of sampling sites in logged management units, also showing different levels of logging roads, and rivers in the landscape. (b) Location of Guyana and the Iwokrama rainforest in South America. (c) Layout of bat and bird mist net and point count stations within sample sites.

measurements were sent to Dr. Brian O'Shea for verification. Bats were identified using a regional field guide (López-Baucells, 2018) and the key in Lim and Engstrom (2001). When necessary, bat identifications were confirmed by Dr. Burton Lim (Assistant Curator of Mammalogy at the Royal Ontario Museum).

Species were categorized according to their respective dietary guild and vertical stratification of forest use. To classify guilds and vertical stratification of birds, we followed Stouffer et al. (2021), but for species that were not listed in that paper, we followed Wilman et al. (2014). Guild classifications for bats followed the regional field guides and Lim and Engstrom (2001).

## 2.5 | Data analysis

We calculated species richness and species diversity using Shannon's diversity ( $H'$ ) index to compare assemblage compositions in each timeframe. The choice of the  $H'$  index was made under the assumption that it may provide another description of the ecosystem diversity opposed to just richness counts, that accounts for the proportions of rare and generalist species across timeframes (Morris

et al., 2014). Additionally, we plotted rarefaction curves with a bootstrap of 50 and a confidence level of 0.95% for each taxa response across each time treatment (Chao et al., 2022). We used non-metric multidimensional scaling (NMDS) from Bray-Curtis dissimilarity metrics to visualize assemblage dissimilarity across timeframes, combined with a multivariate analysis of variance (ADONIS) to test for assemblage level differences. To help understand how species level data can reveal patterns in a post-RIL rainforest, an INDVAL analysis of bird and bat assemblage data was conducted. INDVAL uses a species abundance matrix to examine species affinity (site uniqueness) and fidelity (frequency of occurrence) to a specific site treatment (i.e. logging timeframe; Ne & Legendre, 1997). If a species was noted to be significantly related to one specific timeframe (pre-logged, 1 year post-logged and 10-year post-logged), that species was deemed an indicator (Björklund et al., 2020; Carignan & Villard, 2002; Chen et al., 2020). For conciseness, we report our indicator species findings generally, but expand upon the predominant guild classifications these indicators belong to. We then modelled the abundance of indicators with the highest INDVAL value, and report this finding as a measurement of how disturbance-sensitive guilds/species responded as regeneration progressed.

We appraised timeframe (pre-logged, 1 year after and 10 years after) and harvest intensity as metrics to determine richness changes in birds and bats. Harvest intensity was spatially calculated at four scales in QGIS by creating 100, 200, 500 and 1000m buffers around the sampling point and calculating the number of trees harvested in each buffer per site sampled. The four spatial scales were calculated to assess both local (100 and 200m) as well as landscape (500 and 1000m) levels of impact of harvest on richness change. We conducted all of these analyses across the whole assemblage, and at the level of feeding guild, and vertical stratification of birds (understorey, midstorey, canopy and all levels).

Bayesian multi-level models (BMLMs) were used to determine bird and bat richness with the predictor variables 'timeframe' and 'harvest intensity'. To address how adjacent unlogged areas may affect bird and bat richness through spillover effects, we ran models of richness against a 'distance to primary forest' parameter by measuring the distance (in metres) of the sample sites to the nearest, unlogged management unit. These models found distance to primary forest to have no effect and were not included in final results. We report findings from nine Bayesian models of species richness and one model for indicator species response in our bird and bat data. A partial effects pooling approach was utilized because unique site locations were established and sampled in the larger management unit they were located and thus catered for uncertainty around alpha and beta diversity in each sampling location (Gelman & Pardoe, 2006). All models followed a negative binomial distribution, using weak informative priors to consider all possible outcomes in our posterior distribution. Each model ran for 4000 iterations with a post-warmup sampling of 1000 iterations. Model convergence and accuracy were scrutinized through visual analysis of trace plots and Markov Chain Monte Carlo (MCMC) intervals. We noted high MCMC uncertainty for Sanguinivores and thus do not report them in our discussion. Model comparisons were made through a leave-one-out cross validation (LOOCV) test to determine which model performed best (Bürkner, 2017, 2018). To account for some small differences in survey effort (due to weather), we calculated mist netting effort as the total time mist nets were open over the 3-day period per sample site, and multiplied that by the number of nets open. We then took the (log) effort and included that as our offset term in the 'best' model according to our LOOCV if effort was statistically significant.

Lastly, given the multiple methods employed to sample birds, we anticipated species overlap and as such had two analytical approaches to the bird data. In our first approach we removed overlapping species (those detected by both methods) from the point count dataset before analysis. In our second approach, species overlap was left in the point count dataset. Both approaches led to the same overall conclusions, and therefore we report the findings of our second approach which encompasses a larger dataset. In the results and discussion, we consider the mist net and point count findings separately, while noting that our mist net data are primarily understorey birds, while the point count data encompass birds using all forest levels.

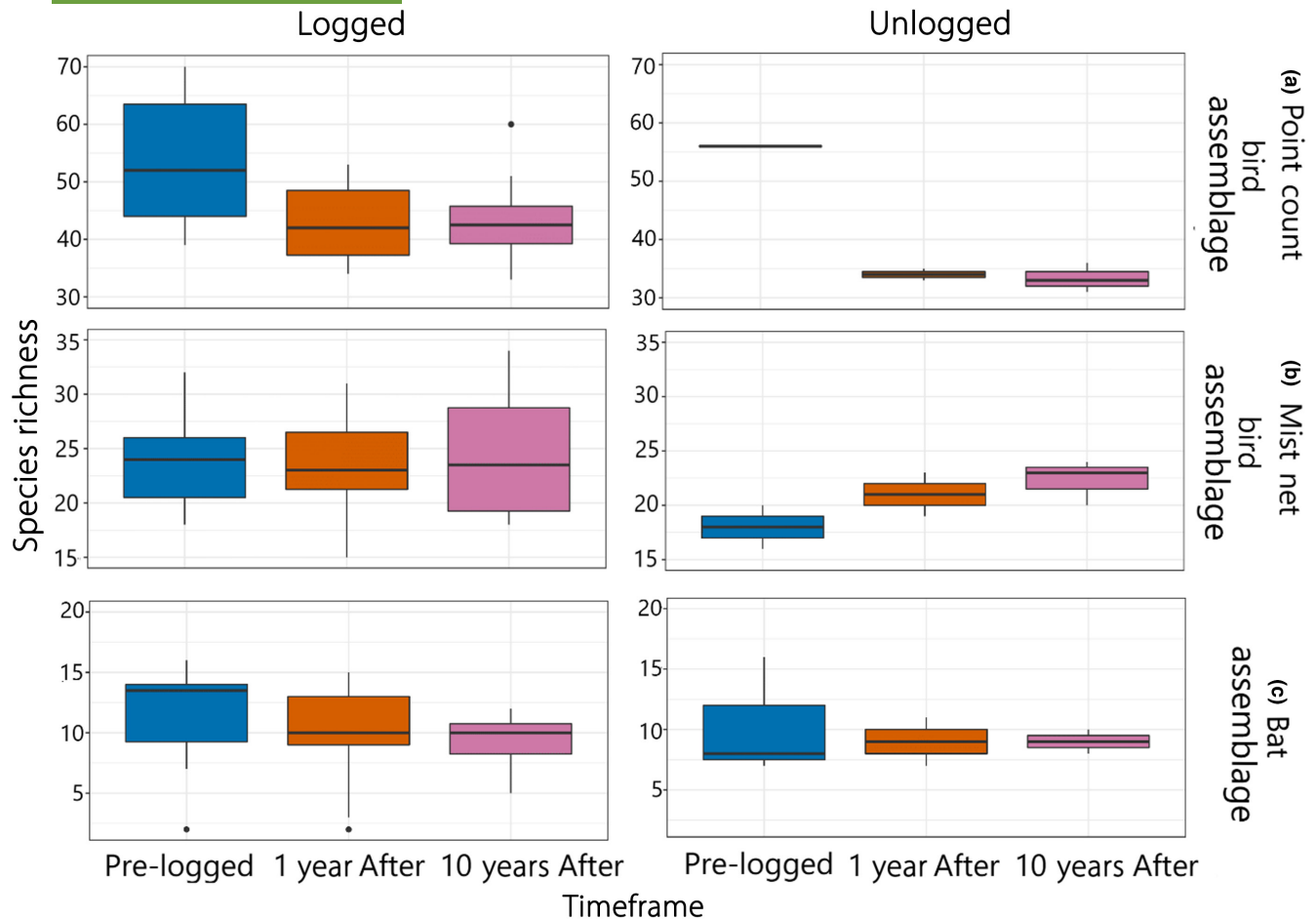
### 3 | RESULTS

Across all logging timeframes, a total of 134 species were recorded in the bird mist net assemblage at the 14 logged sites, and 59 species in the three control sites. The point count data recorded 200 bird species in logged sites and 98 species in control sites. Across both bird datasets, bird species belonged to seven feeding guilds. Across all logging timeframes, 50 bat species were recorded in the logged sites and 24 species in the control sites. Bat species belonged to seven feeding guilds. For the harvest sites, 45% of recorded species were found in the mid-upper vertical foraging positions, 47% were found in the understorey while 9% of birds utilized all vertical foraging positions in the point count data. In the harvest site mist net data, 70% of recorded birds were found in the understorey, 25% in the mid-upper levels and 5% utilized all vertical foraging positions.

Bird species richness (Figure 2) and diversity (Figure S1) in mist net data did not change across all logging timeframes in the logged sites, while in the control sites there was a slight increase over the study timeframe. In contrast, bird species richness and diversity in the point count dataset showed variable changes in both control and logged sites. There was evidence of a decrease in logged sites 10 years after logging compared to pre-logging richness with little to no changes between 1 year after and 10 years after, while there was small increase in the control sites compared to 1 year after. Bat richness (Figure 2) and diversity (Figure S1) decreased 10 years after in logged sites compared to pre-logging, while control sites were mostly stable during the study period. When adjusted for extrapolation, highest species richness in the harvest sites was expected to be recorded in pre-logged and 1 year post-logged for birds found in the understorey and predominantly in pre-logging for mid-upper-level birds. Bat richness was expected to be highest 1 year after logging (Figure S2).

#### 3.1 | Assemblage analyses

Mist net bird assemblage in logged sites differed significantly across the logging timeframes (ADONIS:  $F = 1.97$ ,  $p = 0.001$ ), however, pre-logged and 1 year after logging assemblages were more similar to one another than the 10 years after logging assemblage, which exhibited lower site level variability than in the earlier logging timeframes (Figure 3). There was evidence that point count bird assemblage differed more than the mist net birds (ADONIS:  $F = 3.24$ ,  $p = 0.001$ ), with 10 years after assemblage composition exhibiting a gradual shift away from 1 year after but closer to pre-logging assemblage composition (Figure 3). Compared to the control sites, both mist net bird assemblage (ADONIS:  $F = 1.18$ ,  $p = 0.25$ ) and point count bird assemblage (ADONIS:  $F = 1.55$ ,  $p = 0.025$ ) differed in their assemblage composition, however, only the assemblage change of point count birds in the control sites was significant. The mist net bird assemblage showed high site variability across timeframes in the control sites whereas 1 year after and 10 years after control sites were most similar for point count birds.



**FIGURE 2** Box plots of species richness of birds detected via mist nets and point counts (a and b) and bat (c) assemblages across timeframes. Top panels show change over time in the logged sites, bottom panels show change over time in the control sites that were never logged.

Bat assemblage also differed over the logging timeframe (ADONIS:  $F=2.04$ ,  $p=0.006$ ; Figure 3). As with the mist net bird assemblage, bat assemblage 10years after logging had lower site-level variability than the other logging timeframes. In the control sites, bat assemblage showed a similar response as seen with birds, whereby site variability differed across each timeframe (ADONIS:  $F=1.67$ ,  $p=0.12$ ).

### 3.2 | Indicator species

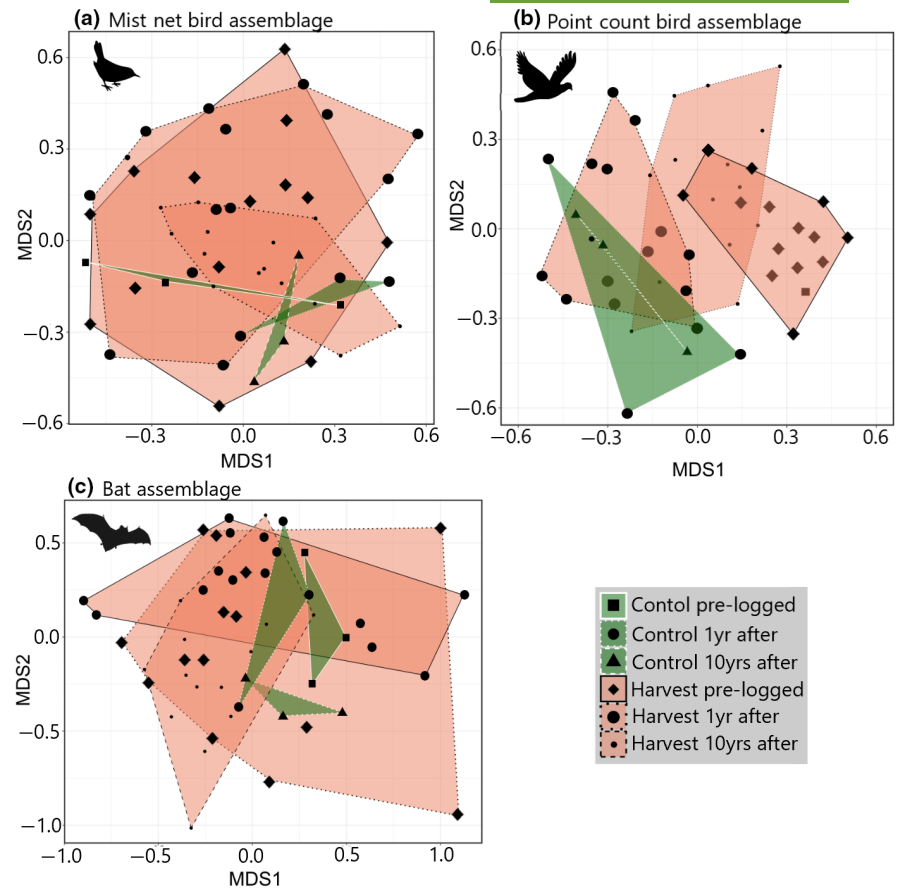
Eight species were identified as indicators among the mist net bird assemblage, whereas 32 species were indicators in the point count data (Table S1), potentially indicating a greater response to logging among the birds inhabiting higher levels of the forest strata. Twenty-two of these were indicators of pre-logging. The Olivaceous Schiffornis (*Schiffornis olivacea*), had the highest indicator value for 10years after mist net birds and the lowest indicator value for 10years after point count birds. When combined, 27 of 40 bird species were insectivores and little over half (25 of 40) occurred in the understorey. Indicators with the highest INDVAL value

were the Dusky Antbird (*Cercomacroides tyrannina*) and the Spot-tailed Antwren (*Herpsilochmus sticturus*) for the pre-logged group, the Cinereous Antshrike (*Thamnomanes caesius*) and the Dusky Parrot (*Pionus fuscus*) for the 1 year after group and the Olivaceous Schiffornis and Variegated Tinamou (*Crypturellus variegatus*) for the 10 years after group. Of the 10 years after indicators, *S. olivacea* is an understorey omnivore while *C. variegatus* is a terrestrial bird, best considered a frugivore or omnivore.

Three species of bats were indicators of logging timeframe—the carnivorous Peters' Woolly False vampire bat (*Chrotopterus auritus*) and the frugivorous flat-faced fruit-eating bat (*Artibeus planirostris*) were both indicators of pre-logged, whereas Palla's long-tongued bat (*G. soricina*), a nectarivore, was an indicator of the 10 years after logging group.

The variation in richness response to timeframe was statistically significant in the bird point count dataset only (Table S3). In terms of harvest intensity, all harvest buffers did not have strong significant effect on overall bird and bat richness (Table S4). Overall, a small amount of the variance in our data could be explained through richness response to timeframe alone, with more variation in the point count data being explained (14%) compared to the mist net (0.09%) and bat data (0.09%) variations.

**FIGURE 3** NMDS ordinations of bird and bat assemblages through timeframes. (a) understorey bird assemblage, (b) mid-upper-level bird assemblage and (c) bat assemblage. Stress values were birds: 0.2 (harvest), 0.08 (control); mist net bird data: 0.2 (harvest), 0.1 (control); point count bird data: 0.2 (harvest), 0.000008 (control).



### 3.3 | Predictive modelling of bird and bat assemblages

Our analyses of the predictors of bird assemblages estimate that as timeframe increased, there was a decline in average richness from pre-logged (CrI: 3.88, 4.06), to 10 years after (CrI: -0.34, -0.08) in point count birds, whereas mist net birds had no noticeable change in recorded richness by 10 years after logging (CrI: -0.16, 0.18) (Table S3). A similar decline in richness was noted for bats from pre-logged (CrI: 2.28, 2.63) to 10 years after (CrI: -0.50, 0.04), however, only point count birds had a statistically significant change in richness 10 years after logging. Sampling locations in harvest sites were not a good predictor of overall richness changes for both taxa (mist net birds: CrI: -0.37, 0.56; point count birds: CrI: -0.46, 0.18; bats: CrI: -1.10, 0.22) as timeframe increased. In terms of feeding guild, granivorous birds recorded in mist net data showed a small, negative correlation to trees harvested in 100m (CrI: -9.30, -0.06) and 500m (CrI: -1.17, -0.01), whereas the 100m buffer had a small, positive correlation on mist net omnivorous birds (CrI: 0.01, 0.21), and an additional small, positive correlation at 1000m buffer on carnivorous bats (CrI: 0.02, 1.02) (Table S6).

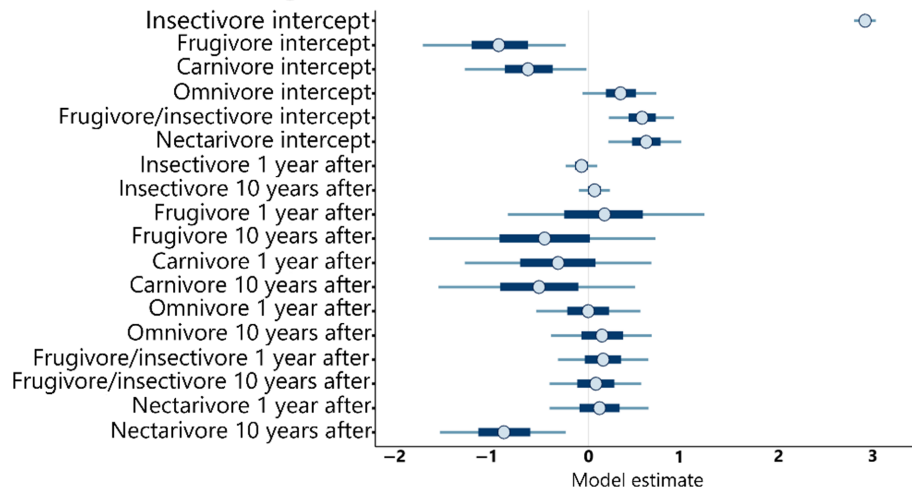
Feeding guild and stratification were both significant predictors of the changes in bird and bat richness as timeframe increased (Table S5). By 10 years after logging, nectarivores declined in both mist net and point count datasets (mist net data: CrI: -1.68, -0.12;

point count data: CrI: -2.38, -0.21), whereas insectivores declined in point count birds only (CrI: -0.42, -0.08). Bat richness had a similar decline for carnivorous species (CrI: -3.28, -0.55) as timeframe increased (Figure 4). In terms of stratification, canopy bird richness in both datasets (mist net birds: -1.38, -0.06; point count birds: CrI: -0.43, -0.08) declined 10 years after logging (Figure 5).

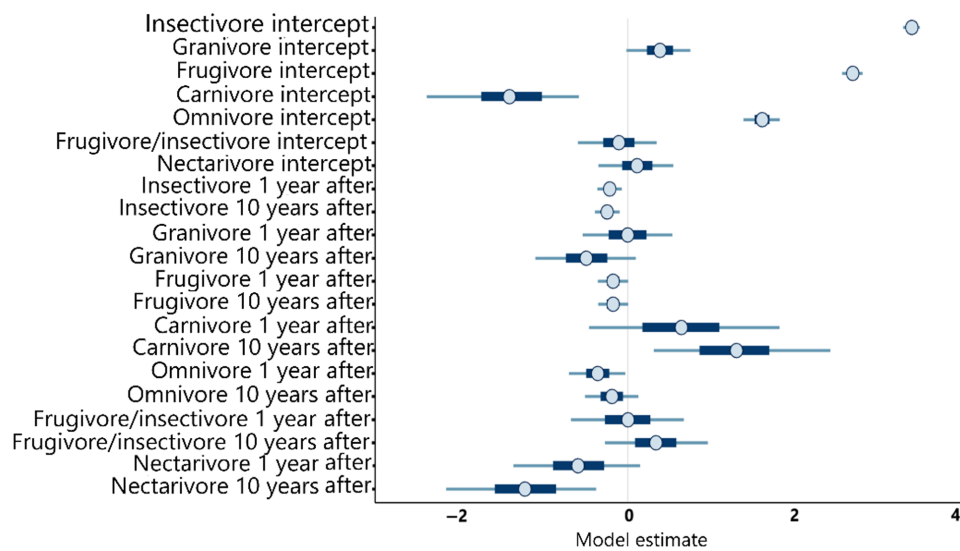
Further analysis of indicator species with the highest INDVAL values showed four mist net bird indicators had higher estimated abundance 10 years after (*Schiffornis olivacea*: CrI: 2.84, 36.7; *Thamnophilus murinus*: CrI: 0.33, 2.44; *Sclerurus mexicanus*: CrI: 1.99, 44.30; *Myiobius villosus*: CrI: 1.52, 56.02) whereas one indicator further decreased in abundance after 10 years (*Myiobius barbatus*: CrI: -34.45, -0.64). For point count birds, three indicators decreased in estimated abundance 10 years after (*Herpsilochmus sticturus*: CrI: -44.36, -3.80; *Tolmomyias assimilis*: CrI: -41.35, -3.41; *Chlorophanes spiza*: CrI: -35.05, -3.43) while one species increased in estimated abundance (*Crypturellus variegatus*: CrI: 0.57, 1.76). For the bat assemblage, two indicators declined in estimated abundance 10 years after (*Cauritus auritus*: CrI: -5.76, -0.96; *Artibeus planirostris*: CrI: -1.90, -0.28) whereas one indicator increased in estimated abundance (*Glossophaga soricina*: CrI: 1.57, 6.88) (Table S2).

LOOCV tests determined that timeframe and harvest had the greatest predictive power of changes in richness (Table S7). The probabilities of non-negligible effects of timeframe on assemblage changes were 51% for mist net birds, 59% for point count birds and

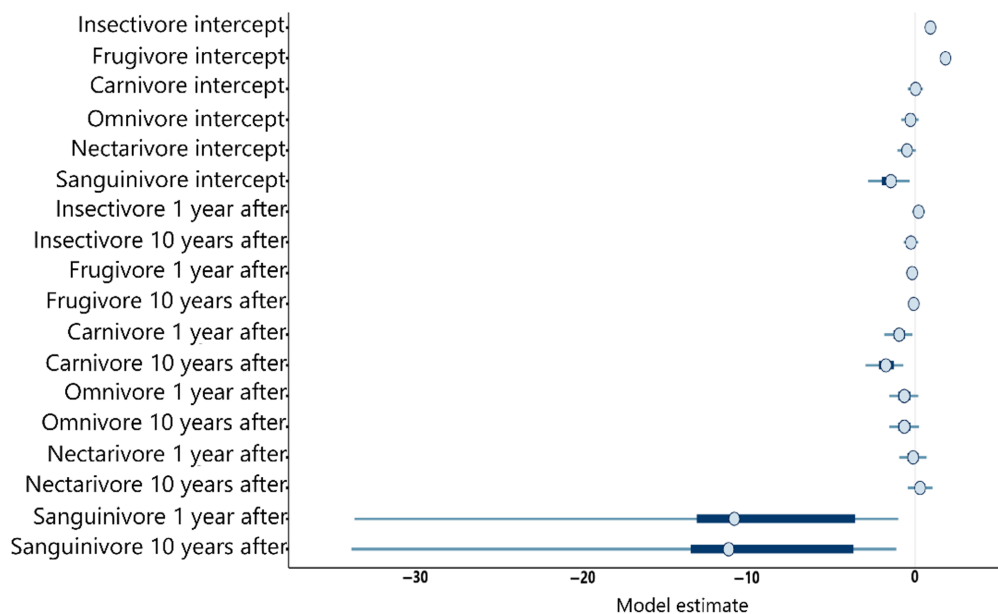
## (a) Mist net bird assemblage



## (b) Point count bird assemblage



## (c) Bat assemblage



**FIGURE 4** Markov Chain Monte Carlo (MCMC) interval plots of effect of timeframe on feeding guilds in bird (a and b) and bat (c) assemblages. Light blue dot represents mean, thick blue bars represent 50% credibility intervals, thin blue lines represent 95% credibility intervals.

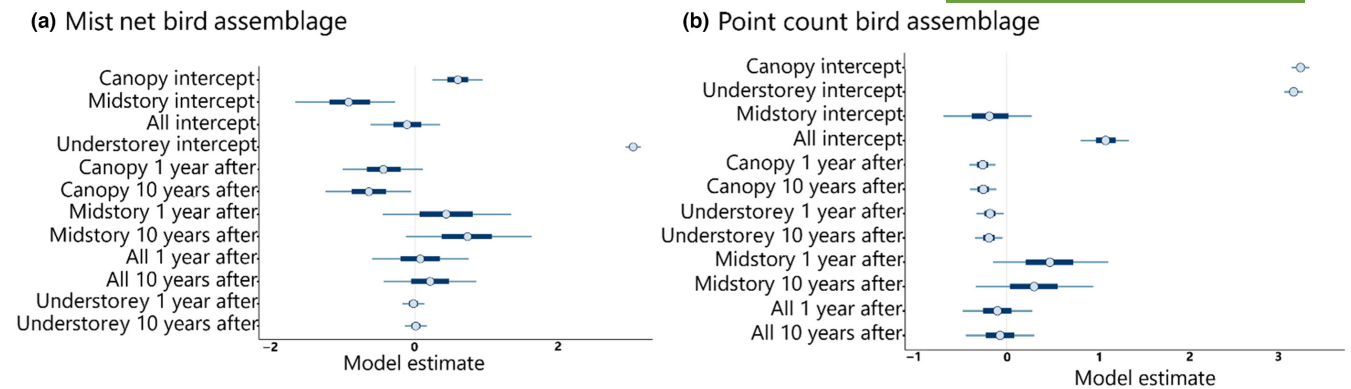


FIGURE 5 Markov Chain Monte Carlo (MCMC) interval plots of effects of timeframe on stratification in (a) mist net and (b) point count bird assemblages. Light blue dot represents mean, thick blue bars represent 50% credibility intervals, thin blue lines represent 95% credibility intervals.

84% for bats. Furthermore, the incorporation of log effort as a predictor in this model did not result in a change in previous inferences for mist net birds and bat richness, but had a positive effect on point count bird richness (CrI: 0.01, 1.64).

#### 4 | DISCUSSION

Our study contributes new information to a vital research gap on the longer-term effects of RIL on biodiversity in tropical forests. We find that most species are still retained after RIL, consistent with previous studies; however, because we measured biodiversity at two points after RIL, we find that shorter-term studies to date may underestimate eventual species responses to RIL for certain niches. Given that species richness and diversity are positively correlated with vegetation density (Felton et al., 2006), floral diversity (Wells et al., 2007) and percentage canopy cover in disturbed rainforests (Blonder et al., 2018; Philip et al., 2018; Silveira & Azevedo-Ramos, 2009), it has been proposed that low-harvest intensity and increased regeneration time (~30–60 years) can help resolve harvest-related impacts on assemblage change. In the specific case of RIL managed rainforests like that in our study system, active efforts to close off and monitor the post-harvest landscape may be beneficial in ensuring richness retention. Our data analysis revealed that timeframe was useful in explaining both bird and bat assemblage change in terms of species richness, thus offering further credibility to the implementation of regeneration times that span longer than 10 years. Compared to the short-term assessments in the same landscape by Bicknell, Gaveau, et al. (2015) and Bicknell, Struebig, and Davies (2015), our results showed a small decline in overall richness from pre-logged to 10-year post-logged for point count birds and a decrease in nectarivores, insectivores, canopy birds and carnivorous bats related to time since logging, explain more than half of the observed changes in the faunal assemblage. Additionally, there were notable changes in richness between pre-logged and 10 years after in control sites for the bird assemblages (mist net and point count). Birds have been shown to increase in richness as logging

intensity increases (Burivalova et al., 2014). This phenomenon also implies that total species richness in logged sites can go above that of control sites, indicative by the relative richness of habitat generalists versus specialists (Burivalova et al., 2014; Paillet et al., 2010; Woltmann, 2003), thus potentially explaining the observed increase in richness in control sites for mist-netted birds. In contrast, given that Iwokrama mandates sites be closed only after harvest, vegetative complexity of logged sites may differ from the control. Different patches of logged forest may offer different resources (Burivalova et al., 2014; Sekercioglu, 2012), resulting in some species (i.e. frugivores and nectarivores) being able to successfully forage in RIL forest while choosing to nest in its control sites. Although we do not present data on guild changes from the control sites, the fluctuations seen in control site richness could be the result of natural turnover due to factors not associated with logging impacts.

Canopy birds were noted to decline in both bird datasets. Rainforest birds that forage in the mid-upper rainforest levels can be specialized physiologically to different microclimate conditions compared to understorey birds (Thiollay, 1992). Stratford and Stouffer (2015) proposed that species found in mid-upper strata may increase their numbers in early post-harvest RIL stands, but decline in logged rainforests once canopies begin to close as regeneration progresses. Although our findings support this assumption, these results may also indicate the onset of local extinction debt—loss of species due to changes in environmental or demographic variability, long after disturbance has ceased (Cooke et al., 2019; Kuussaari et al., 2009). When compared to the pre-logged richness, there was a noticeable decline in species as timeframe increased, with richness change correlating with canopy birds and insectivores and nectarivores. Furthermore, indicator species that showed high fidelity and uniqueness to RIL rainforests 10 years after logging occurred mainly in the understorey, further implying a shift in physiological response in favour of the understorey rainforest levels.

Changes in stratification of forest use can be linked to changes in feeding guilds (Bicknell, Gaveau, et al., 2015; Bicknell, Struebig, & Davies, 2015). Our results showed that nectarivores and insectivores had a clear decline over time, omnivorous birds

responded positively to harvest intensity only and carnivorous bats responded negatively to timeframe and had a weak, positive response to harvest intensity. Stratification of forest use is influenced by functional traits such as body size or trophic position and the dominance of these traits can be further linked to resource competition at different rainforest stratifications (Burivalova et al., 2014; Hamer et al., 2015; Pillay et al., 2019). Our data indicate that insectivore richness had the most negative response while nectarivore richness declined the least, however, nectarivore decline in both the understorey and mid-upper levels, has been observed elsewhere in selectively logged rainforest (Felton et al., 2008; Gray et al., 2007; Wunderle et al., 2006). Research in Asia and the Neotropics highlight that nectarivores make up a small percentage of overall avian species, and an increase followed by a decrease in nectarivore richness has been linked to patterns of flower availability following logging (Gray et al., 2007). Given that nectar production and flowering diminish as shade-intolerant flora are outcompeted in regenerating rainforest (Felton et al., 2006), nectarivores may have less foraging success as resources change with regeneration, leading to their overall decline in both understorey and mid-upper-level richness.

Insectivores, on the other hand, tend to occupy higher trophic positions in tropical rainforests, and as such, changes in numbers can be linked to shifts in invertebrate populations, changes in microclimate and possibly body size adaptability (Gutiérrez-Granados & Dirzo, 2021; Hamer et al., 2015), hence their higher sensitivity to disturbance. We identified eight insectivore bird indicators for the 10 years after timeframe, with seven occurring in the understorey. Three of these indicator species can be further classified as terrestrial insectivores: *S.mexicanus* (tawny-throated leaf-tosser), *C.variegatus* (variegated tinamou) and *F.analis* (black-faced Antthrush) (Stouffer et al., 2021), two of which increased in abundance as timeframe increased in logged sites. Terrestrial insectivores are deemed most sensitive to habitat change (Powell et al., 2015; Stratford & Stouffer, 1999), but it has also been proposed that a small number of terrestrial insectivores may persist from low-impact disturbances (Boyle & Sigel, 2015; Stratford & Stouffer, 2015). Additionally, terrestrial insectivores have narrow microhabitat preferences (Bicknell & Peres, 2010; Borges, 2013; Cintra & Naka, 2011) that are often associated with shallow leaf litter and a greater density of canopy cover (Stratford & Stouffer, 2013). When placed in the context of a low-impact RIL forest that was left to regenerate for 10 years, the identification of these terrestrial insectivores as indicators, as well as their increased abundance 10-year post-harvest, highlights the potential of RIL forests to regain species that may be associated with primary forest. Moreover, among the most recorded species were understorey army-ant followers such as *P.albifrons* (white-plumed antbird) and *G.rufigula* (rufous-throated antbird), as well as *M.brachyura* (Pygmy antwren) which is known to follow mixed-species flocks (Wilman et al., 2014) and was also an indicator species for 10-year post-logged. Army-ant followers and mixed-species flocks represent a collection of generalist

and specialist feeders that have shown both negative (Azevedo-Ramos et al., 2006; Felton et al., 2008; Henriques et al., 2008; Mestre et al., 2020) and positive (Laurance et al., 2004; Schleuning et al., 2011) responses to anthropogenic disturbance. The reasons behind these trends may be linked to different intensities of selective logging resulting in fluctuations in insect assemblage (Burivalova et al., 2014; Gustafsson et al., 2012), with some researchers indicating that insect diversity increases with changes to understorey vegetation complexity in disturbed sites due to increased solar radiation to the forest floor (Langellotto & Denno, 2004). Alternatively, Ewers et al. (2015) and Burghouts et al. (1997) proposed the opposite, whereby invertebrate abundance and diversity decreases with changes to forest floor characteristics such as litterfall and forest floor decomposition. Furthermore, the presence of an indicator species that forages in mixed-species flocks in 10-year post-logged, may be indicative of shifts in richness in favour of species that follow the same ecological niche (i.e. generalists), and can evade predation better (Thiollay, 1999). More importantly, mixed-species flock foraging becomes relevant in understanding how the ecological niches for other species shift as time progresses as the presence of flocks has the potential to influence the fitness and distribution of species that participate in mixed-flock foraging (Harrison & Whitehouse, 2011; Jullien & Thiollay, 1998). This dynamic can cause flocks to alter entire bird assemblages (Goodale et al., 2015), which becomes important to investigate as regeneration progresses in a low-impact RIL forest.

Both nectarivore and insectivore declines can thus be linked to foraging behaviours, which have changed with regeneration. This response may be a delayed interaction that indicates the realization of extinction debts. The Olivaceous Schiffornis (*S.olivacea*) was noted to occur as an indicator of both mist net and point count birds for 10 years after logging and was the only omnivorous indicator species. Schiffornis birds exhibit 'manakin-like' behaviours including broad diets and may benefit from canopy enclosure.

Overall, declines observed in richness were not due to harvest intensity, though based on our model results, we argue that harvest intensity had a small influence on shifts in omnivorous birds and carnivorous bats. However, 10 years after logging saw most guilds being retained or recovered to a state similar to pre-logging levels in the bird point count assemblage. The fluctuations may indicate that despite reductions in richness which reflect a state of relaxation for some niches, recovery may be co-occurring for other niches. Additionally, as regeneration progressed, mid-upper-level bird assemblage became more similar to pre-logged assemblage, further indicating the retention of most species in the post-harvest landscape. We consider this finding an important indication that low-harvest RIL forests have the ability to retain faunal populations despite ecological fluctuations. We also find evidence of extinction debts realized up to 10 years after logging in mid-upper-level birds that would not have been detected had we only surveyed immediately after logging, and these are likely acting alongside other

factors such as the natural the turnover seen in Bicknell, Gaveau, et al. (2015) and Bicknell, Struebig, and Davies (2015) from the same landscape. Additionally, a current challenge relating to the extinction debt debate is the assumption that species richness was in equilibrium before the disturbance impact (Kuussaari et al., 2009). The findings from Iwokrama's 10-year post-RIL rainforest offer a compelling argument for the implementation of mandatory closure of harvest blocks to allow adequate regeneration (>10 years), which has shown to be important for mammal richness in the same forest (Harris, Hallett, et al., 2023), and warrants the incorporation of longer-term population databases into the management and examinations of RIL-logged forests. We know that time since logging explained >50% of the assemblage change in birds, but more than 80% in the bat assemblage, further emphasizing the importance of monitoring the effects of disturbances over the long term.

#### AUTHOR CONTRIBUTIONS

Jake E. Bicknell conceived the idea and designed the methodology; Arianne E. Harris and Jake E. Bicknell collected the data along with the field team; Arianne E. Harris conducted the data analysis with contributions from Jake E. Bicknell and Anand Roopsind. Brian J. O'Shea, Jake E. Bicknell, Anand Roopsind, Gyanpriya Maharaj, Matthew Hallett and Raquel Thomas contributed critically to the drafts and gave approval for publication, which Arianne E. Harris led.

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#### CONFLICT OF INTEREST STATEMENT

We the authors verify no affiliations with or involvement in any organization, nor are there any competing interests with any financial interest (such as honoraria; participation in speakers' bureaus; membership, employment, consultancies, stock ownership or other equity interest; and expert testimony or patent-licensing arrangements), or non-financial interest (such as personal or professional relationships, affiliations, knowledge or beliefs) in the subject matter or materials discussed in this manuscript.

#### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are publicly available via Zenodo Digital Repository: <https://zenodo.org/doi/10.5281/zenodo.10040900> (Harris, Maharaj, et al., 2023).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Figure S1.** Box plots of species diversity ( $H'$ ) of birds detected via bird mist net and point counts (A & B) and bat (C) assemblages across timeframes. Left column shows change over time in the logged sites. Right column show change over time in the control sites that were never logged (unlogged).

**Figure S2.** Rarefaction curves showing extrapolated species richness across timeframes for bird mist net, point count and bat assemblages.

**Table S1.** Indicator species analysis of understory bird assemblage, mid-upper-level bird assemblage and bat assemblage data across the three timeframes.

**Table S2.** Model output for richness response to timeframe only in understory bird, mid-upper-level bird and bat indicator species with highest INDVAL value. Non-overlapping credibility intervals (CrI) indicate certain effect.

**Table S3.** Model output for richness response to timeframe only in understory bird assemblage, mid-upper-level bird assemblage and bat assemblage. Non-overlapping credibility intervals (CrI) indicate certain effect.

**Table S4.** Model output for richness response to timeframe + harvest buffers in understory bird assemblage, mid-upper-level bird assemblage and bat assemblage. Non-overlapping credibility intervals (CrI) indicate certain effect.

**Table S5.** Model output for feeding guild + Stratification response to timeframe in understory bird assemblage, mid-upper-level bird assemblage and bat assemblage. Non-overlapping credibility intervals (CrI) indicate certain effect.

**Table S6.** Model output for feeding guild response to timeframe + harvest buffers in understory and mid-upper-level bird assemblages and bat assemblage. Non-overlapping credibility intervals (CrI) indicate certain effect.

**Table S7.** Leave-one-out cross validation (LOOCV) test on bird (understory and mid-upper-level) and bat assemblages response models.

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